

The Development of the Hermaphroditic Gonad in Four Species of Dicyemid Mesozoans

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ABSTRACT—The development of the functionally hermaphroditic gonad, the infusorigen, in four dicyemid species, *Dicyema orientale*, *D. acuticephalum*, *D. japonicum*, and *D. misakiense*, was studied in fixed materials with the aid of a light microscope. After an agamete (axoblast) undergoes the first division and excludes a paranucleus, the resulting cell undergoes the second division. Afterwards, three different types of cell lineage can be identified. (1) In *D. orientale*, the first oogonium is produced by the second division, and the axial cell of an infusorigen and the first spermatogonium are produced by the third division. (2) In *D. acuticephalum*, the first oogonium is produced by the second division, the axial cell is produced by the third division, and the spermatogonium is produced by the fourth division. The fourth division also produces the first oogonium of another egg line. (3) In *D. japonicum* and *D. misakiense*, the first spermatogonium is produced by the second division, and the axial cell and the first oogonium are produced by the third division. In all species examined, oogonia occupy the outer surface of the axial cell and spermatogonia are incorporated into the axial cell. In this way, the spermatogenesis proceeds within the cytoplasm of the axial cell. Mature infusorigens of these four species consist of about twenty cells. The respective numbers of oocytes and spermatozoa produced in each infusorigen are roughly equal in these four species.

INTRODUCTION

Dicyemid mesozoans are found in the renal sac of benthic cephalopod molluscs. The bodies of dicyemids consist of only 20 to 40 cells and they are organized very simply [12, 14]. It has long been debated whether dicyemids are truly primitive multicellular animals [2, 7, 8, 11, 17], or whether they are actually organisms that have degenerated as a result of parasitism [5, 12, 14, 19].

As well known, two kinds of adult forms, nematogens and rhombogens, are found in dicyemids. Asexual reproduction occurs within the axial cell of a nematogen, while sexual reproduction takes place within the axial cell of a rhombogen. The features of the sexual reproduction are unique [12, 15]. A hermaphroditic gonad, which is called an infusorigen, is formed within the axial cell of a rhombogen, and fertilization occurs around the

infusorigen. The zygote undergoes cleavages and develops into an infusoriform larva within the axial cell. The process of the fertilization and embryogenesis of infusoriforms have been described in detail [1, 3, 18], but the development of infusorigens has been studied only sporadically [10, 12, 14]. No research on the patterns of development of infusorigens has been performed from a systematic perspective. We examined the development of the infusorigens of *Dicyema orientale*, *D. acuticephalum*, *D. japonicum*, and *D. misakiense*, and found three different types of cell lineage. In this report, these three different cell lineages that can be followed during the development of infusorigens are described. In addition, we provide an estimate of the numbers of gametes that are produced and of the numbers of embryos that are generated in one infusorigen, and we discuss the reproductive capacity of infusorigens.

MATERIALS AND METHODS

Seventeen individual octopuses, *Octopus vulgaris*, and three cuttlefish, *Sepioteuthis lessoniana*, were purchased or collected by the authors in the waters off the western coast of Japan. *Dicyema orientale* from *Sepioteuthis lessoniana* and three species of dicyemids, namely, *D. acuticephalum*, *D. japonicum*, and *D. misakiense*, from *Octopus vulgaris* were examined in the present study.

After the host cephalopods had been sacrificed, their renal sacs were taken out and smeared directly on glass slides. Smeared dicyemids were immediately fixed with Carnoy's fixative or with alcoholic Bouin's solution (a mixture of absolute ethanol saturated with picric acid, formalin and acetic acid, 15:5:1, v/v). Specimens fixed with Carnoy's fixative were stained with Feulgen's stain

or by the PAS method and were poststained with Ehrlich's hematoxylin and light green. Specimens fixed with alcoholic Bouin's solution were stained with Ehrlich's hematoxylin and light green only. The development of infusorigens in the axial cells of rhombogens was observed with the aid of a light microscope under an oil-immersion objective at a final magnification of 2000 diameters.

RESULTS

Dicyema orientale (Figs. 1, 2, 7, and Table 1)

At the stage of the transition from the nematogen to the rhombogen, a number of agametes (axoblasts) degenerate. The remaining agametes, that number about 10 to 20, grow larger and

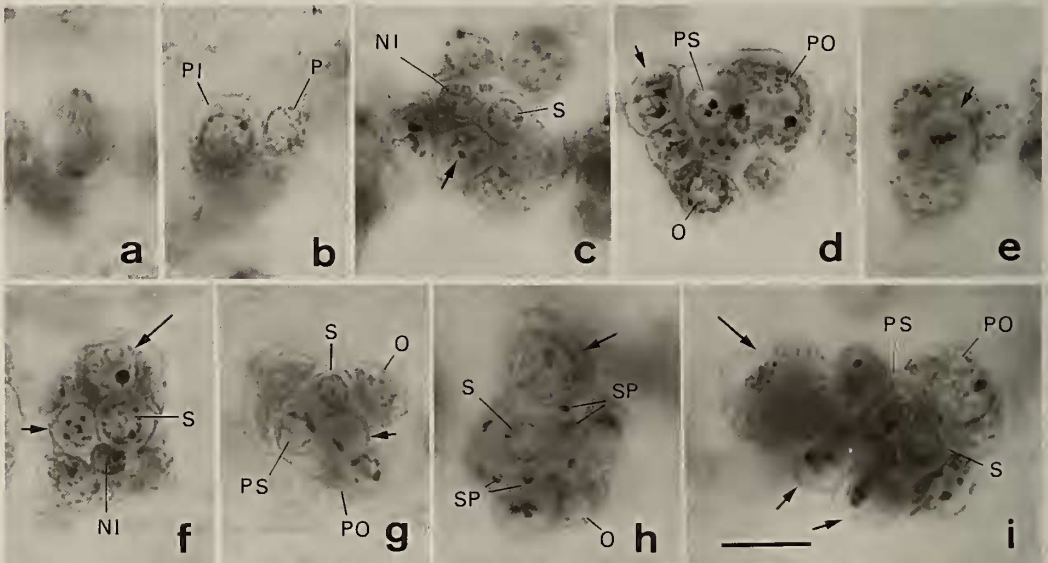


FIG. 1. Light micrographs of developing infusorigens within the axial cells of rhombogens of *D. orientale*. Photographs were taken at a magnification of 2000 diameters under an oil-immersion objective. Scale bar represents 10 μm . (a): An agamete undergoing an unequal first division. (b): A progenitor cell of an infusorigen (PI) and a paranucleus (P) being produced after the first division. (c)-(i): Infusorigens. (c): The arrow indicates the zygote stage of a primary spermatocyte. (d): The arrow indicates the zygote stage of a primary oocyte. (e): The arrow indicates the metaphase of a primary spermatocyte. (f): The short arrow indicates the metaphase of a secondary spermatocyte viewed from the pole and the long arrow indicates the pachytene stage of a primary oocyte. The nucleolus is conspicuously large in the primary oocyte at the pachytene stage. (g): The arrow indicates the metaphase of a secondary spermatocyte viewed from the side. (h): The arrow indicates the diplotene stage of a primary oocyte. (i): The short arrows indicate the bouquet stage of a primary oocyte and the long arrow indicates the anaphase of a primary oocyte. NI, axial cell nucleus of infusorigen; O, oogonium; PO, primary oocyte; PS, primary spermatocyte; S, spermatogonium; SP, spermatozoon.

undergo an unequal division (Fig. 1a). Each smaller daughter cell loses its cytoplasm and becomes just a nucleus, known as a paranucleus, and it lies near the cell from which it arose (Fig. 1b). The

paranucleus stays within the axial cell of the rhombogen and grows to the same size as the axial cell nucleus of the rhombogen. The larger daughter cell, namely, the progenitor of the infusorigen,

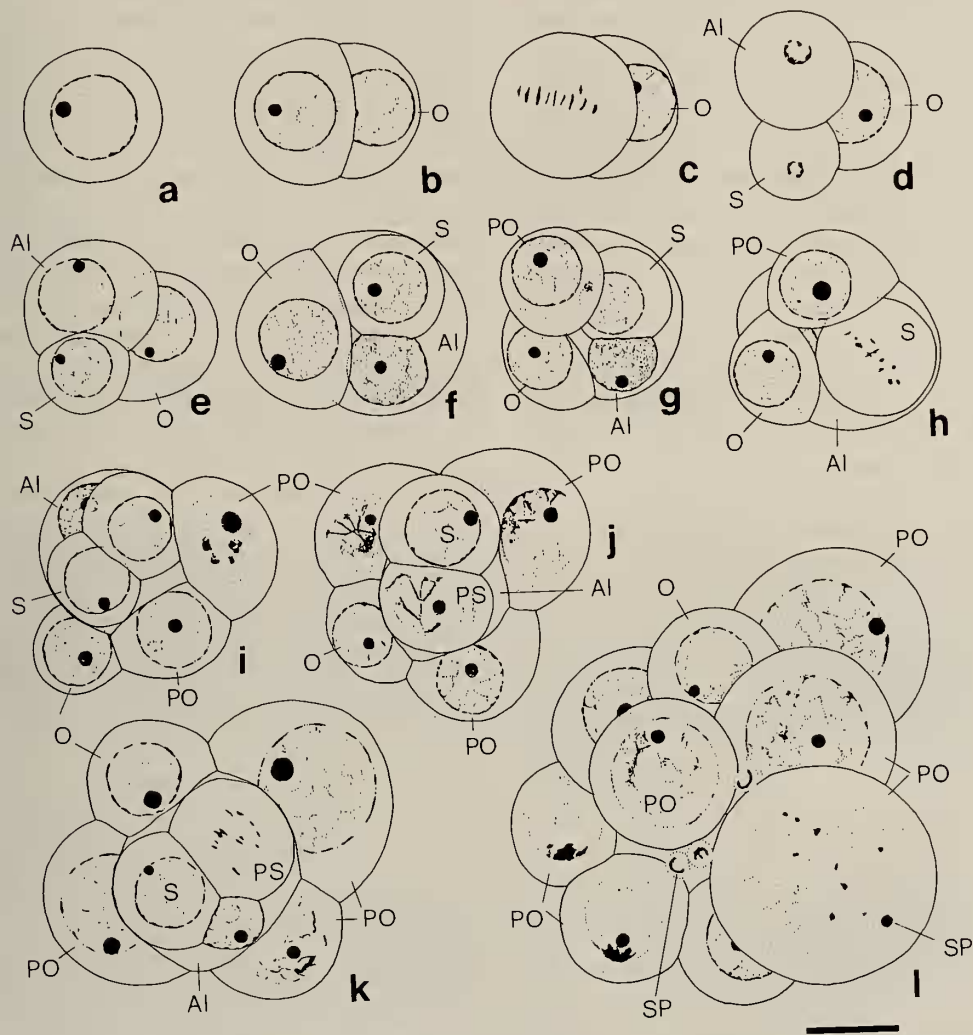


FIG. 2. Sketches of the development of the infusorigen of *D. orientale*. Bar represents 5 μ m. (a): A progenitor cell of infusorigen. (b) and (c): Two-cell stage. In (c), the metaphase of the third division is seen. (d)-(f): Three-cell stage. In (d) and (e), both the axial cell (AI) and the first spermatogonium (S) produced after the third division are shown. In (f), the first spermatogonium (S) is embedded in the axial cell (AI). (g): Four-cell stage. (h): Five-cell stage. The metaphase of the first spermatogonium (S) is seen. (i): Six-cell stage in optical section. (j): Eight-cell stage in optical section. Primary oocyte (PO) at the upper right corner is in the zygotene stage. (k): Nine-cell stage in optical section. The anaphase of the primary spermatocyte (PS) is seen. (l): The infusorigen. A primary oocyte (PO) at the beginning of anaphase is seen in the lower right corner. This oocyte contains a spermatozoon (SP) in the cytoplasm. Spermatozoa (SP) in the center are emerging from the axial cell of the infusorigen.

AI, axial cell of infusorigen; O, oogonium; PO, primary oocyte; PS, primary spermatocyte; S, spermatogonium; SP, spermatozoon.

undergoes a nearly equal division to the two-cell stage (Figs. 2b and c). One of these cells becomes the first oogonium. The other cell undergoes an equal division and produces the first spermatogonium and an axial cell of the infusorigen (Figs. 2c-e). The axial cell of the infusorigen does not divide further, but it increases in size and incorporates the spermatogonium into its cytoplasm (Fig. 2f). The first oogonium remaining on the periphery of the infusorigen divides equally to generate a second oogonium and a primary oocyte (Fig. 2g). In the same way, the second oogonium produces a third oogonium and a primary oocyte. Very early primary oocytes can be distinguished from oogonia since the nucleolus in the former is larger than that in the latter (Figs. 2g and h). In primary oocytes, at the prophase of the first meiotic division, the chromatin becomes aggregated on one side of the nucleus and the nuclear membrane becomes indistinct on the side opposite the aggregation of chromatin (Figs. 1i and 2l). These features are characteristic of the so-called "bouquet stage" of the prophase of the meiotic division. The primary oocytes gradually become larger and chromosomes become visible as thick threads in the nuclei, features that characterize the zygotene stage. At this stage, both ends of the chromosomes are attached to the nuclear envelope (Figs. 1d and 2j). During the pachytene stage, the chromosomes become indistinct and the nucleus becomes similar in appearance to the interphase nucleus. At this stage, the nucleus includes a very large nucleolus (Figs. 1f and 2k-l). When primary oocytes have grown to about $7\ \mu\text{m}$ in diameter, bead-like chromosomes appear in the nucleus. These oocytes are at the diplotene stage of meiotic prophase (Fig. 1h). The primary oocytes finally reach about $12\ \mu\text{m}$ in diameter (Fig. 1i).

The first spermatogonium within the axial cell of the infusorigen undergoes an equal division and produces a spermatogonium and a primary spermatocyte (Figs. 2h-j). The prophase of the first meiotic division of the primary spermatocyte proceeds similarly to that of the primary oocyte, but the size of the primary spermatocyte does not change throughout the prophase (Figs. 1c, 1d, 2j, and 2k). After the first meiotic division, a pair of secondary spermatocytes enters interkinesis. At

this stage, no chromosome structures can be seen. Within the axial cell of maturing infusorigen, usually two secondary spermatocytes are observed in addition to a spermatogonium and an axial cell nucleus. Soon after the second meiotic division, transformation of spermatids into spermatozoa occurs. Mature spermatozoa are composed of a small amount of deeply stained chromatin and a surrounding small clear area, interpreted as cytoplasm. The cell membrane is hardly visible. The entire spermatozoon is about $2\ \mu\text{m}$ in diameter. The chromatin is usually horseshoe-shaped, but sometimes it is irregularly ring- or dot-shaped (Figs. 1h and 2l). After emerging from the axial cell of an infusorigen, the spermatozoon enters the primary oocyte (Fig. 2l). Fertilized oocytes remain adhering to the axial cell up to the time at which the first polar bodies are produced. Spermatozoa often adhere to the outer surface of the axial cell, to the oogonia, or to the primary oocytes, or they may appear between the oocyte and the axial cell (Fig. 2l). The spermatozoon within the oocyte lies at the periphery of the metaphase plate of the first meiotic division of the oocyte (Fig. 2l). The first polar bodies are composed of a mass of chromatin and a clear cytoplasmic area that is surrounded by a delicate membrane. They become detached from the oocytes and often remain intact, but finally they degenerate.

The numbers of spermatogonia and primary spermatocytes, the number of spermatozoa within and on the surface of the infusorigen, and the numbers of oogonia and primary oocytes per infusorigen are shown in Table 1. *D. orientale*, being relatively long, has a large number of infusorigens and infusoriform embryos in the axial cell of a rhombogen (Table 1).

Dicyema acuticephalum
(Figs. 3, 4, 7, and Table 1)

One or rarely two agametes become larger and undergo an unequal division at the beginning of the rhombogen stage (Figs. 3a and 4a). The larger daughter cell is the progenitor of an infusorigen, while the smaller cell becomes a paranucleus (Fig. 3b). The progenitor cell of the infusorigen undergoes an equal division, which results in the two-cell

TABLE 1. The numbers of infusorigens, gametes, and embryos within the axial cells of rhombogens

Species	Body length of rhombogens (mm)	No. of infusorigens per rhombogen	No. of spermatogonia and primary spermatocytes per infusorigen ¹⁾
<i>Dicyema orientale</i> ²⁾	~3.5	7-25	3.27±0.71
<i>D. acuticephalum</i>	~0.8	1- 2	3.38±0.86
<i>D. japonicum</i>	~1.0	1- 2	4.06±1.28
<i>D. misakiense</i>	~1.0	1- 2	4.04±1.24

Species	No. of spermatozoa per infusorigen ¹⁾	No. of oogonia and primary oocytes per infusorigen ¹⁾	No. of infusoriform embryos per rhombogen
<i>D. orientale</i> ²⁾	11.78±5.21	10.26±2.30	~250
<i>D. acuticephalum</i>	12.67±4.70	9.25±1.43	~ 20
<i>D. japonicum</i>	10.00±3.91	13.43±3.47	~ 35
<i>D. misakiense</i>	11.59±4.70	12.04±3.76	~ 35

¹⁾ Values represent means±S.D. and are based on results from 50 mature infusorigens.

²⁾ *D. orientale* was described only with nematogens [16] and no rhombogens have been reported.

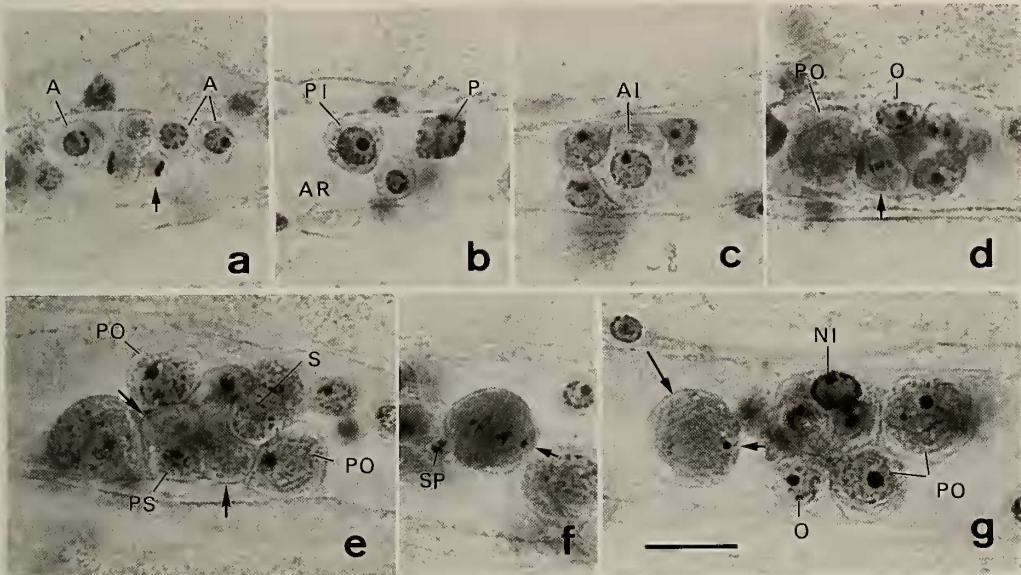


FIG. 3. Light micrographs of developing infusorigens within the axial cells of rhombogens of *D. acuticephalum*. Bar represents 10 μ m. (a): Agametes (A). A telophase figure of the first unequal division is seen in the center. The arrow indicates a smaller daughter cell that becomes a paranucleus. (b): A progenitor cell of an infusorigen (PI) and a paranucleus (P) within an axial cell (AR) of a rhombogen. (c): Five-cell stage. (d)-(g): Infusorigens. (d): The arrow indicates the metaphase of a primary spermatocyte viewed from the side. (e): The arrows indicate the interkinesis stage of the secondary spermatocytes. (f): The metaphase of a primary oocyte viewed from the side. The arrow indicates a sperm within the oocyte. (g): The large arrow indicates the anaphase of a secondary oocyte. The short arrow indicates a sperm within it. The primary oocyte (PO) is at the pachytene phase. AI, axial cell of infusorigen; NI, axial cell nucleus of infusorigen; O, oogonium; PO, primary oocyte; PS, primary spermatocyte; S, spermatogonium; SP, spermatozoon.

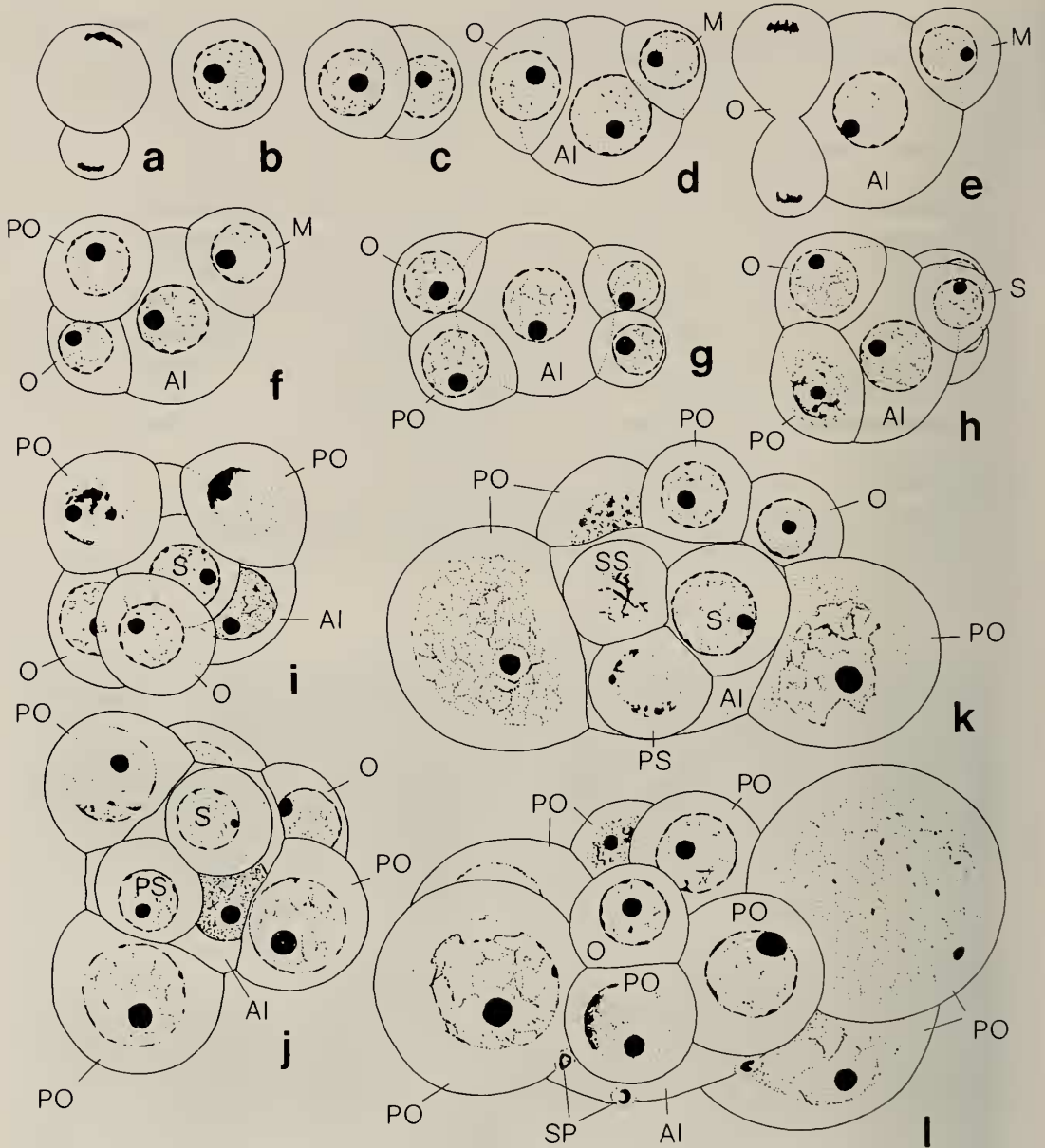


FIG. 4. Sketches of the development of the infusorigen of *D. acuticephalum*. Bar represents $5\ \mu\text{m}$. (a): The telophase of the first division of the agamete. The smaller cell becomes a paranucleus. (b): The progenitor cell of an infusorigen. (c): Two-cell stage. (d)-(e): Three-cell stage. In (e), the telophase of an oogonium (O) is seen. The cell marked M is a mother cell of an oogonium and a spermatogonium. (f): Four-cell stage. (g): Five-cell stage. Two cells on the right side of the axial cell, produced by the division of the mother cell (M in e and f), become the first spermatogonium and the oogonium of one egg line, respectively. (h)-(i): Six-cell stage. In (i), the first spermatogonium (S) is embedded in the axial cell (AI) and the primary oocytes (PO) are at the bouquet stage. (j): Eight-cell stage in optical section. (k): An infusorigen in optical section. A secondary spermatocyte (SS) is seen in the axial cell (AI). (l): An infusorigen (surface view). The anaphase of a primary oocyte (PO) is seen in the upper right corner.

AI, axial cell of infusorigen; M, mother cell of the first spermatogonium and the oogonium; O, oogonium; PO, primary oocyte; PS, primary spermatocyte; S, spermatogonium; SP, spermatozoon; SS, secondary spermatocyte.

stage (Fig. 4c). One of these cells becomes the first oogonium, and the other cell increases in size and divides unequally. The larger cell, the axial cell of the infusorigen, undergoes no further divisions (Fig. 4d), while the smaller cell divides equally and produces both the first spermatogonium and an oogonium (Fig. 4g). Both cells are so similar in size and appearance that they cannot be distinguished until one of them enters the mitotic phase on the periphery of the infusorigen or is embedded in the axial cell (Fig. 4i). *D. acuticephalum* has two egg lines (Fig. 7B). The oogonium of each egg line further divides and generates an oogonium and a primary oocyte (Figs. 4e-i). At around the six-cell stage, the first spermatogonium is incorporated into the axial cell of the infusorigen (Fig. 4i). The process of spermatogenesis is similar to that observed in *D. orientale*. The chromatin of spermatozoa usually forms a horseshoe or an irregular ring (Fig. 4l). The numbers of spermatogonia and primary spermatocytes, and other numerical data, are shown in Table 1.

Dicyema japonicum and *Dicyema misakiense*
(Figs. 5-7 and Table 1)

The developmental pattern of the infusorigen is the same in *D. japonicum* and *D. misakiense*. One or rarely two of the agametes become larger and undergo an unequal division at the beginning of the rhombogen stage. The smaller cell is transformed into a paranucleus, while the larger cell becomes the progenitor of an infusorigen (Fig. 5a). This latter cell divides unequally and produces two cells (Figs. 5b and 6a). The smaller cell often undergoes an equal division (Fig. 6b), but one of the daughter cells soon degenerates. The remaining cell is the first spermatogonium (Fig. 6c). The larger cell divides equally and, thus, produces the first oogonium and an axial cell of the infusorigen (Figs. 5c and 6d). The axial cell undergoes no further divisions and increases in size. The first spermatogonium is incorporated into the cytoplasm of the axial cell (Fig. 6e) and its nucleus increases in size (Fig. 6f). The oogonium gives rise

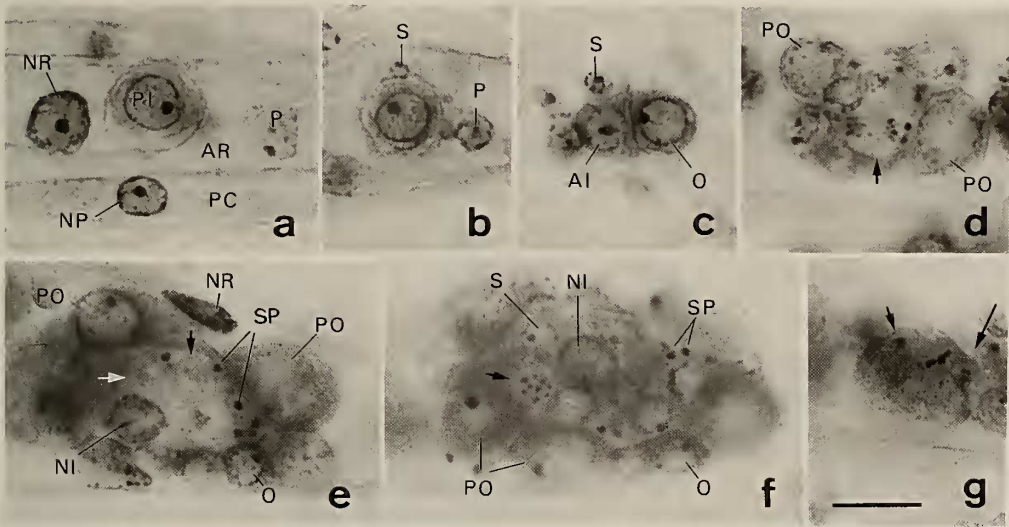


FIG. 5. Light micrographs of developing infusorigens within the axial cells of rhombogens of *D. japonicum*. Bar represents 10 μ m. (a): A progenitor cell of an infusorigen (PI), the axial cell of a rhombogen (AR), a peripheral cell nucleus (NP), an axial cell nucleus of a rhombogen (NR), a paranucleus (P), and peripheral cell cytoplasm (PC) can be seen. (b): Two-cell stage. (c): Three-cell stage. (d)-(f): Infusorigens. (d): The arrow indicates the metaphase of the primary spermatocyte. (e): The arrows indicate the interkinesis stage of a secondary spermatocyte. (f): The arrow indicates the metaphase of a secondary spermatocyte viewed from the pole. (g): The telophase of a primary oocyte. The long arrow indicates the first polar body. The short arrow indicates the sperm within the primary oocyte. AI, axial cell of infusorigen; NI, axial cell nucleus of infusorigen; NR, axial cell nucleus of rhombogen; O, oogonium; P, paranucleus; PO, primary oocyte; S, spermatogonium; SP, spermatozoon.

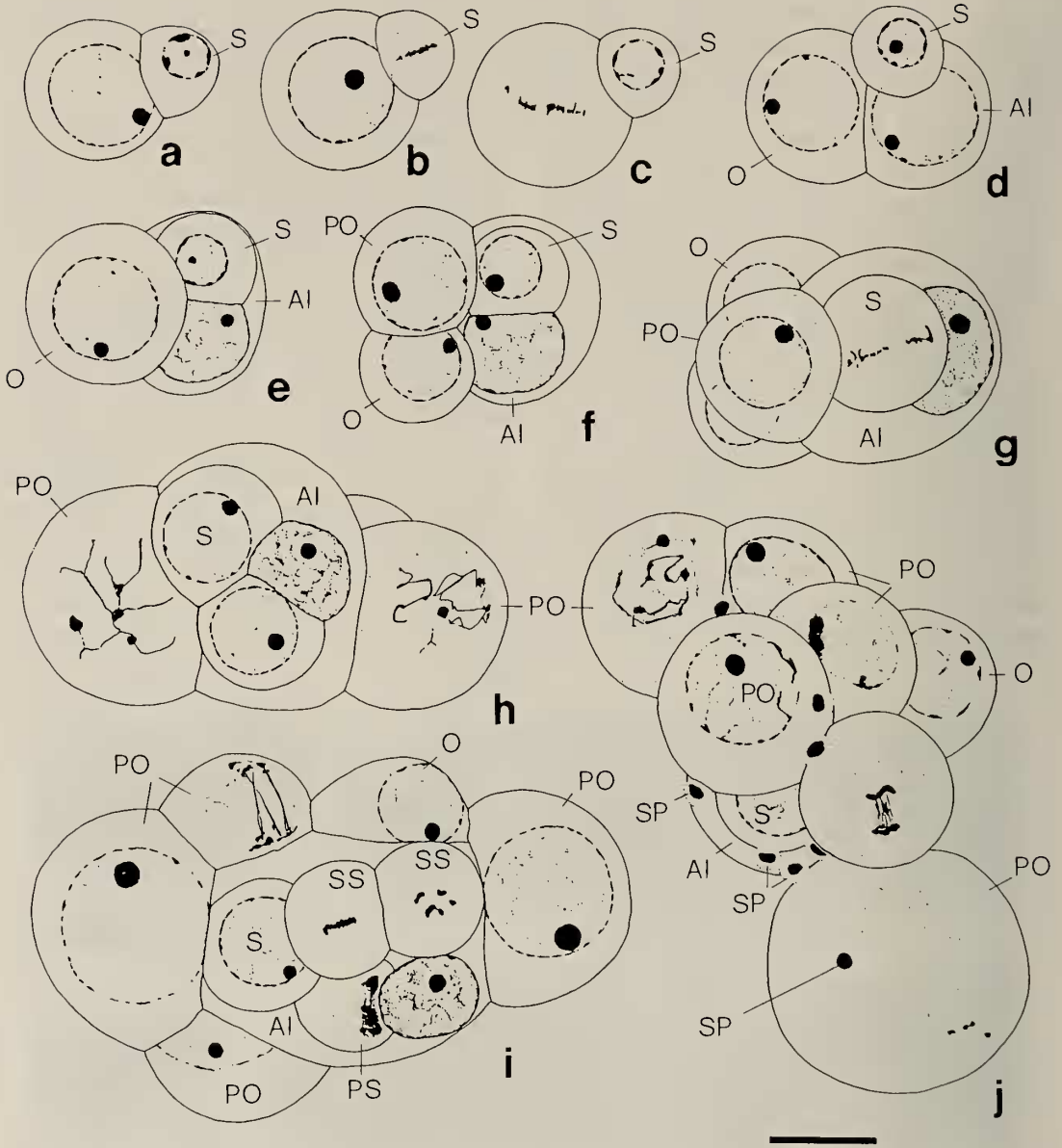


FIG. 6. Sketches of the development of infusorigens of *D. misakiense*. Bar represents 5 μm . (a)-(c): Two-cell stage. As seen in (b), the first spermatogonium (S) often divides quite early. In (c), the mother cell of both the first oogonium and the axial cell is in metaphase. (d)-(e): Three-cell stage. In (e), a spermatogonium (S) is embedded in the axial cell (AI). (f): Four-cell stage. (g): Five-cell stage. The metaphase of a spermatogonium (S) is seen. (h): Eight-cell stage in optical section. The primary oocytes (PO) at the zygotene stage are seen. (i): The infusorigen in optical section. The primary oocytes (PO at the left and right) at the pachytene stage and another oocyte (PO at the upper left corner) at the zygotene stage are seen. The metaphases of the secondary spermatocytes (SS) are also seen from the side (center) and from the pole (right). (j): The infusorigen (surface view). Some spermatozoa (SP) are emerging from the axial cell. AI, axial cell of infusorigen; O, oogonium; PO, primary oocyte; PS, primary spermatocyte; S, spermatogonium; SP, spermatozoon; SS, secondary spermatocyte.

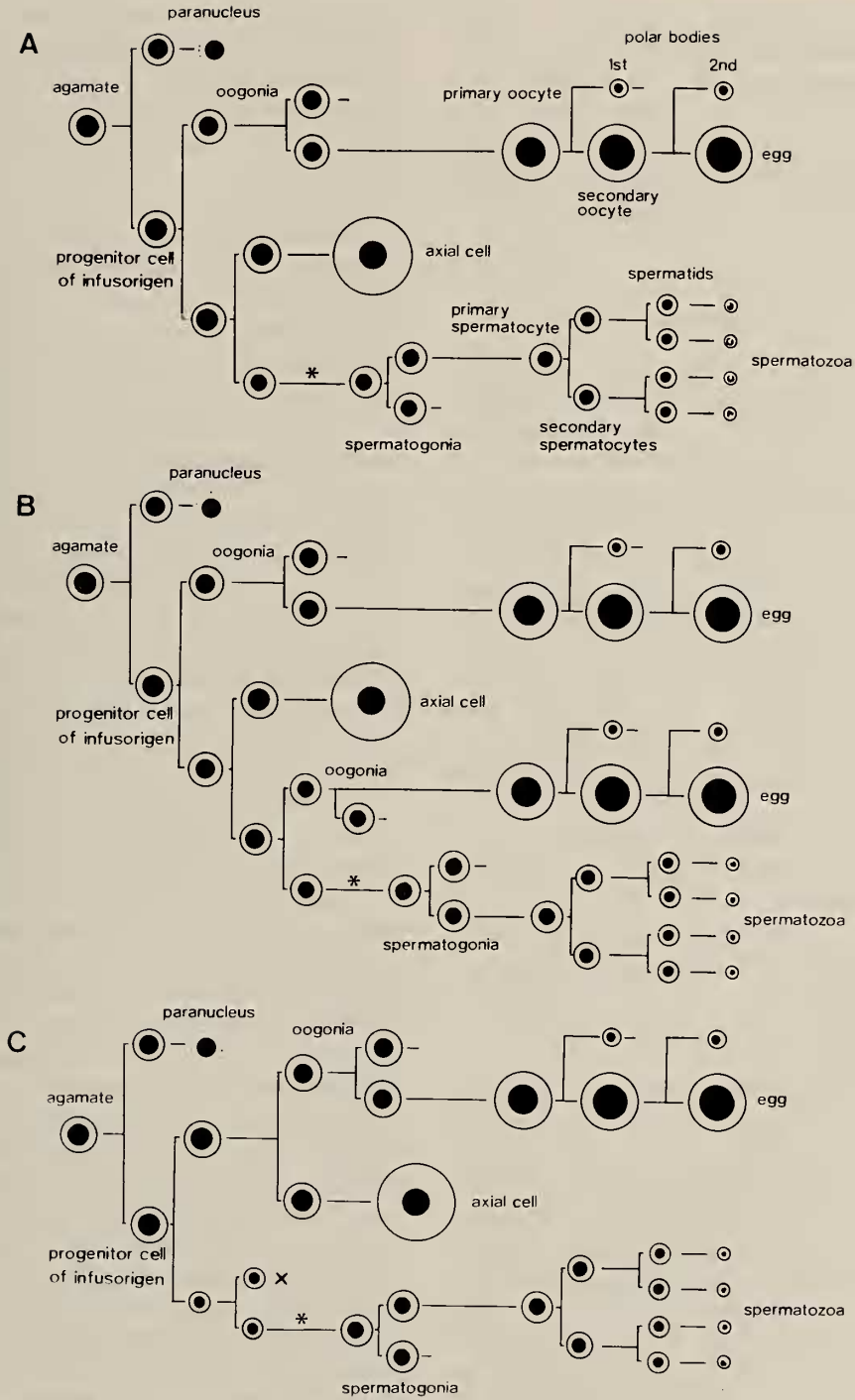


FIG. 7. The cell lineage of an infusorigen. (A): *D. orientale*. (B): *D. acuticephalum*. (C): *D. japonicum* and *D. misakiense*. The circle represents the cell and the central black area represents the nucleus. They are nearly scaled. The dotted circle means that the cytoplasm degenerates. At the site of the asterisk (*), the first spermatogonium is embedded in the axial cell. Short horizontal lines on right side of cells indicate that the cells proliferate further. In (c), the cross (x) means that the cell does not proliferate but degenerates.

to a new oogonium and a primary oocyte. Subsequent oogenesis and spermatogenesis proceed in the same manner as in *D. orientale* and *D. acuticephalum*. The nucleus of the spermatozoa is horseshoe- or dot-shaped, and the spermatozoa often aggregate (Figs. 5e, 5f, and 6j). The number of spermatozoa and other numerical data are shown in Table 1.

DISCUSSION

In the four species of dicyemid mesozoans studied herein, an agamete enlarged at the beginning of the rhombogen stage. In other species of dicyemids, Nouvel [14] and McConnaughey [12] also reported that an agamete enlarges at the very early stage of the rhombogen. This enlargement is interpreted as a sign of the beginning of the development of infusorigens. Then the agamete undergoes an unequal division and the smaller daughter cell becomes a paranucleus without contributing to the formation of an infusorigen. Although we can offer no explanation for the formation of a paranucleus, it is a constant feature and may, thus, be essential to the development of infusorigens.

Several differences were apparent in the cell lineage of the infusorigens of the four species (Fig. 7). Nevertheless, two common features were apparent; one is that the first spermatogonium is incorporated into an axial cell, in which spermatogenesis proceeds; and the other is that the oogonium remains at the periphery of the axial cell, where oogenesis occurs. The distinctive differences occur early in the development in the various species. Two patterns of cell lineage are distinguishable. One pattern is characterized by a second division that produces the first oogonium, and the other is characterized by a second division that produces the first spermatogonium. The former is seen in *D. orientale* and *D. acuticephalum*, and the latter in *D. japonicum* and *D. misakiense* (Fig. 7). In *D. orientale*, *D. japonicum*, and *D. misakiense*, all types of cell differentiate up to the third division. In *D. acuticephalum*, by contrast, spermatogonia are generated only after the fourth division (Fig. 7B). In spermatogenesis, all four species examined have only one sperm line. In

oogenesis, *D. acuticephalum* has two egg lines, while the other three species have only one (Fig. 7). However, *D. acuticephalum* has a rather small number of oogonium and oocytes (Table 1). The body size may be a factor that limits the number of oocytes.

The development of infusorigens was reported by Lameere [10], Nouvel [14], and McConnaughey [12]. Lameere studied *D. typus*, while McConnaughey did not specify the species that he studied. However, both these authors observed that the first oogonium is produced by the second division and the first spermatogonium and axial cell are generated after the third division. This previously reported cell lineage is, thus, the same as that observed in *D. orientale*. Nouvel [14] traced the development of the infusorigen of *D. schulzianum*. His findings are identical to ours in *D. japonicum* and *D. misakiense* in that the first spermatogonium is produced after the second division and the oogonium and axial cell are produced after the third division. However, the first spermatogonium of *D. schulzianum* is relatively large compared to that of *D. japonicum* and *D. misakiense*. In *D. orientale*, *D. japonicum*, and *D. misakiense*, the first spermatogonia, formed by unequal divisions, are relatively small before they are incorporated into an axial cell. They increase in size until they are as large as oogonia after having been incorporated into an axial cell. In *D. acuticephalum*, the first spermatogonium is also a small-sized cell. The third division in this species proceeds unequally and generates a larger axial cell and a smaller cell. This smaller cell is the mother cell of both the first spermatogonium and the oogonium of one egg line. Thus, the differentiation of the first spermatogonium occurs later in *D. acuticephalum* than in the other species (Fig. 7). The pattern of cell lineage observed in *D. acuticephalum* has not been reported in the earlier literature. Although previous reports dealing with a few species [10, 12, 14] did not pay any attention to species-specific differences in the cell lineages of infusorigens, a distinct difference does exist and could be a criterion for classification of dicyemid species.

In *D. japonicum* and *D. misakiense*, the presumptive first spermatogonium often undergoes equal division before being incorporated into the

axial cell. However, one of the daughter cells degenerates soon without differentiating into an oogonium, in contrast to the case in *D. acuticephalum*. This particular division might be an "extra" cell division because it does not occur consistently in all infusorigens examined.

In *D. aegira*, which is about 1.5 mm in total length and has one or two infusorigens, two to three times as many spermatozoa are produced as oocytes [1, 13]. Among the species studied herein, *D. orientale* is a relatively large dicyemid, reaching 3.5 mm in length, and it has 7 to 25 infusorigens. *D. acuticephalum*, which is small, and *D. japonicum* and *D. misakiense*, which are medium-sized, have usually one, or sometimes two infusorigens [4, 16]. In the four species that we examined, the numbers of spermatozoa and the numbers of the oogonia and primary oocytes were roughly equal (Table 1). The numbers of oogonia and primary oocytes were 2.7 to 3.3 times those of spermatogonia and primary spermatocytes. If spermatogenesis and oogenesis proceed at the same rate during the germ cell division and maturation, the number of spermatozoa can be estimated to be 13 to 16 (3.27 to 4.06×4). These values are 1.2 to 1.5 times the values for oocytes. This discrepancy may be attributed to a possibly lower rate of spermatogenesis than of oogenesis [1]. The apparently small number of spermatozoa might be due to the limited space within the axial cell of the infusorigen. A large number of spermatozoa may not be necessary in dicyemids, which perform self-fertilization within the axial cells of rhombogens. However, it is still unclear why the present four species have much smaller numbers of spermatozoa than *D. aegira*. It is apparent that the size of rhombogens and the number of infusorigens per rhombogen do not affect the number of gametes produced.

In the nematode *Caenorhabditis elegans*, the cell lineage of the gonad has been studied in detail [6, 9]. Dicyemids have very simple gonads that are composed of a very small number of cells, and thus, they may also prove to be useful as model systems for studies of the differentiation of gametes.

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